

The contribution of poplar plantations to regional diversity of ground beetles (Coleoptera: Carabidae) in agricultural landscapes

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The PAMUCEAF (Poplars — A multiple-use crop for European arable farmers) project of the European Union was initiated to evaluate the influence of poplars on local agricultural practice and on local and regional biodiversity. The underlying hypothesis was that afforestation with poplars contributes to regional biodiversity. We use ground beetles as an indicator taxon and show that poplar plantations contain mainly ubiquitous species with unspecific habitat requirements. Judged by the samples from pitfall traps the species numbers in the poplar plantations were lower than in the adjacent arable land and did not noticeably contribute to overall regional diversity. An analysis of community structure revealed that the plantations did not contain habitat specialists not occurring elsewhere in the adjacent rural environments. We have no convincing evidence that the plantations enhanced species numbers in adjacent fields by providing refuges or hibernation sites.

Introduction

Diversification away from traditional farm enterprises has become essential to the viability of many farm businesses and rural communities. In this respect farm forestry might be an attractive alternative (BioMaTNet 2002). However, most trees have relatively long rotation terms of 50 or more years; a fact that limits potential farm incomes. For farm afforestation to be a successful enterprise, rotation terms of trees should be short (Dinus 2000). Poplars (*Populus* spp.) meet these criteria. In Poland they have been planted since the beginning of the 19th century (Czarnecki 1996). Today, new genetically modi-

fied poplar trees promise even faster growth and better timber quality (Strauss 1999, Campbell 2000). The PAMUCEAF (Poplars — A multiple-use crop for European arable farmers) project of the European Union embedded into the FAIR program of Framework V (FAIR6-CT98-4193) aims at evaluating the potentials of poplars planted on abandoned arable fields.

Arable fields are generally held to be less diverse than natural or semi-natural habitats (Andow 1991, Tivy 1993, Firbank *et al.* 1996, Gurr *et al.* 2003, but see Kleijn *et al.* 2001 and Pfiffner & Luka 2003). Afforestation should therefore contribute to regional diversity. On the other hand, it is well known that agricultural

fields attract arthropod predators due to the higher phytophage densities even when the completion of whole life cycles is possible there for only some species. In this respect a mix of fields surrounded by forests might have a complementary effect (French *et al.* 2001). Forests might serve as refuges or overwintering sites especially for arthropod predators like vagrant spiders, ground and rove beetles, centipedes, and parasitoids that migrate into the fields for prey or host search (Sotherton 1984, 1985, French 1998). Duelli and Obrist (2003) even estimated that up to 63% of all animal species living in agricultural landscapes depend directly on the presence of natural or at least seminatural habitat islands.

The present study focuses on ground beetles (Carabidae) as an often-used indicator taxon for biodiversity (Thiele 1977, Desender *et al.* 1994, Stegner 1999). A series of studies showed that ground beetles were abundant on arable land (Thiele 1977, Lövei & Sunderland 1996, Stegner 1999) and that they readily migrate from surrounding boundary habitats into the agricultural fields (Duelli *et al.* 1990, French *et al.* 2001). Carabidae are known to hibernate in grassy field margins, hedgerows, or forest edges (Nentwig 1995, Thomas *et al.* 2001). Duelli and Obrist (2003) speculate that even seminatural forests or grassland strips might be sufficient to enhance local biodiversity by supplying sites for hibernation or rescue. Species depending on those sites should be rather ubiquitous and generalists. Additionally, Turin and Den Boer (1988), Desender and Turin (1989), Millán de la Peña *et al.* (2003), and Kotze and O'Hara (2003) showed that such species are more likely to survive after changes in land use due to their ability to disperse and to tolerate agricultural landscapes.

In this study we examine whether Carabidae of agricultural landscapes accept poplar plantations as a local refuge and whether poplars have a positive effect on regional biodiversity. We compare the local fauna of two winter wheat fields in northern Poland with the fauna of two adjacent poplar plantations.

Materials and methods

Two ca. 60-year-old poplar (*Populus canescens*)

plantations (Ostromecko (13 ha) and Wierzbiczany (11 ha)) and two adjacent winter wheat fields (Wierzbiczany (8 ha): Ostromecko (6 ha)) near Bydgoszcz in northern Poland were sampled in 2001 with standard Barber traps (Work *et al.* 2002) with a diameter of 7 cm. Cyzmann (2002) provided a detailed phytosociological description of both sites and classified the Ostromecko site as a *Ficario-Ulmetum campestris* and the Wierzbiczany site as a *Tilio-caroinetum stachyetosum*. They are situated in the Vistula lowland and are characterized by rather high levels of groundwater that cause infrequent flooding of both poplar plantations. At each of the four sites we ran 15 traps in form of a transect for one week each in May, June, July and September in accordance with the PAMUCEAF recommendations for standard trapping. The traps at the end of the field transects were about 50 m apart from the margins of the plantations. Both plantations are surrounded by nearby mixed deciduous forests.

We used an indirect method to assess the potential biodiversity effect of poplar plantations. Under the hypothesis that habitat specialists dominate local faunas we expected marked differences in faunal composition between agricultural fields and forests. If species migrate between forests and fields faunal overlap should be significantly higher. As a null model with which we compared observed faunal overlap we assumed a random placement model where local species numbers result from random samples out of a larger regional species pool. Under this hypothesis the probability of finding k common species in two samples (sites) m and l out of a regional species pool n is (W. Czarnacki pers. comm.)

$$p_k = \frac{\binom{n}{k} \binom{n-k}{m-k} \binom{n-m}{l-k}}{\binom{n}{m} \binom{n}{l}} \quad (1)$$

In Eq. 1, k depends on the pool size n . We estimated n from the sample distribution using the non-parametric first and second order jackknife estimators and used EstimateS 6 (Colwell 2000) and EcoSim 7.00 (Gotelli & Entsminger 2002) for constructing species accumulation curves and for estimating species numbers. Standard deviations resulted in all cases from 50 reshufflings of sample order. To assess the

stability of the jackknife estimators a parametric asymptotic linear model (Ulrich 1999), the Monod function (Keating 1998) and an asymptotic power function model (Ulrich 1999) were fitted to the jackknife estimate — sample size curve. The above models are defined by:

$$S_s = \frac{aN + b}{1 + \frac{aN + b}{S_{\text{pool}}}} \quad \text{asymptotic linear} \quad (2)$$

$$S_s = \frac{NS_{\text{pool}}}{a + N} \quad \text{Monod function} \quad (3)$$

$$S_s = \frac{a}{N^z + \frac{a}{S_{\text{pool}}}} \quad \text{asymptotic power function} \quad (4)$$

with S_s being the species number of the sample of size N , S_{pool} the species pool size to be estimated, and a , b , and z the model parameters to be estimated by the fitting algorithm. For parameter estimation we used in all cases the quasi Newton algorithm of the non-linear estimation module of Statistica 5 (Statsoft 1997).

As a second method to assess differences in species composition between the four study sites we used the nestedness temperature calculator (Atmar & Patterson 1995) and compared measured nestedness of the four sites with the estimation from 1000 randomizations. The method analyses whether the faunal composition of different study sites form perfect subsamples from a larger common species pool (a nested pattern) or whether local peculiarities occur. Additionally, species co-occurrence patterns were studied from standardized effect sizes of three commonly used indices, the C-score, the checkerboard score, and the species combination score (Gotelli 2001), obtained from randomized presence-absence matrices as provided by EcoSim 7.00 (Gotelli & Entsminger 2002). We used fixed sum row and column constraints and the sequential swap algorithm for randomization. Standard deviations of effect sizes were computed from 5000 null matrices.

We studied community structures by fitting the sequential breakage model of Sugihara (1980) to our data sets. This model is often used as a null model because a sequential breakage structure is expected in non-interactive commu-

nities where densities are assigned by random processes (Sugihara 1980, Tokeshi 1993, Ulrich 2001). The model is defined by a single shape generating parameter z that defines the resource breakage probability. In the case of a simple random breakage pattern, z should have a value of 0.75 (Sugihara 1980), a log-normal distribution is mimicked from $z = 0.66$ (Ulrich 2002). We used RAD Version 4 (Ulrich 2002) for computing and fitting this model to our data. Standard errors and confidence limits of the model were in all cases based on 100 replicates.

We used Trautner *et al.* (1984) and Hurka (1996) for identification of species. Species names follow Anderson *et al.* (2000), and Luff and Duff (2001). The classification of species into distribution classes and habitat preferences given in Table 1 follows Watała (1995), Hurka (1996), Stegner (1999), and Anderson *et al.* (2000).

Results

Community structure

In total, 994 ground beetles belonging to 52 species were found (Table 1). Because this number is the result of all samples from the four study sites, the respective species accumulation curve (Fig. 1A) should allow the size of the underlying species pool to be estimated. This would be the regional number of species, which are able to colonize the poplar plantations and the adjacent fields. The first and second order jackknife estimators point to 71 and 82 species, respectively (Fig. 1B). However, Fig. 1B shows that these estimates are still not stable but rise continuously with sample size. Fits to the estimate-sample size curve by three asymptotic parametric models (*see above*) instead indicate a lower species pool size of 85 species (asymptotic power function model), 92 species (asymptotic linear model), and 111 species (Monod function), respectively. Most likely, the regional species pool contains at least 90 species.

Using this latter estimate of 90 species we fitted a Sugihara sequential breakage model to the species rank order distribution of the total sample (Fig. 2). This resulted in a breakage probability of 0.76 ± 0.02 . Below, this model serves as a null

Table 1. Species list of ground beetles found in the present study. Status refers to the distribution in Central Europe. Habitat 'open' refers to species common in rather open habitats of agricultural landscapes. Preference 'moist' refers to species preferring rather moist to wet habitat conditions.

Species	Individuals		Status	Habitat	Preferences
	Poplar plantation	Fields			
<i>Agonum muelleri</i> (Herbst)		6	common	open	
<i>Agonum sexpunctatum</i> (L.)		6	common	open	moist
<i>Amara aenea</i> (De Geer)	10	25	common	open	
<i>Amara aulica</i> (Panzer)	3	3	common	open	
<i>Amara communis</i> (Panzer)	2	2	common	open	moist
<i>Amara</i> sp.		9			
<i>Anchomenus dorsalis</i> (Pontoppidan)		1	common	open	
<i>Asaphidion flavipes</i> (L.)		2	common		
<i>Atranus collaris</i> (Menetries)	1		rare		moist
<i>Bembidion articulatum</i> (Panzer)		1	common		moist
<i>Bembidion femoratum</i> Sturm		4	common		
<i>Bembidion lampros</i> (Herbst)	4	16	common	open	
<i>Bembidion</i> sp.	3	18			
<i>Calathus erratus</i> (Sahlberg)	1		common		
<i>Calathus fuscipes</i> (Goeze)		7	common	open	
<i>Calathus melanocephalus</i> L.	2		common	open	
<i>Calathus micropterus</i> Duftschmid		1	common	woodlands	
<i>Carabus auratus</i> L.	4	4	rare	open	
<i>Carabus cancellatus</i> Illiger	10	61		open	
<i>Carabus coriaceus</i> L.		3		woodlands	moist
<i>Carabus granulatus</i> L.	16	12	common		moist
<i>Carabus nemoralis</i> Mueller	8		common	woodlands	
<i>Carabus violaceus</i> L.		1		woodlands	
<i>Chlaenius nigricornis</i> (F.)	2	2	common	woodlands	moist
<i>Clivina fossor</i> (L.)		2	common		moist
<i>Cychrus caraboides</i> (L.)	1			woodlands	
<i>Dolichus halensis</i> (Schaller)		4	common	open	dry
<i>Dyschirius globosus</i> (Herbst)		2	common		moist
<i>Dyschirius</i> sp.	3	2			moist
<i>Elaphrus cupreus</i> Duftschmid	2		common	open	moist
<i>Epaphius secalis</i> Paykull	1		common		moist
<i>Harpalus affinis</i> (Schränk)	2	5	common	open	dry
<i>Harpalus latus</i> (L.)	1		common		
<i>Harpalus rubripes</i> (Duftschmid)	1		common	open	
<i>Nebria brevicollis</i> (F.)	40		common		
<i>Notiophilus biguttatus</i> (F.)		1	common		
<i>Notiophilus</i> sp.		1			
<i>Patrobus atrorufus</i> (Ström)		1	common		moist
<i>Platynus assimilis</i> (Paykull)	67		common	woodlands	moist
<i>Platynus dorsalis</i> (Pontoppidan)		1		open	
<i>Poecilus cupreus</i> (L.)		51	common	open	
<i>Poecilus versicolor</i> (Sturm)	1	32	common	open	
<i>Pseudoophonus griseus</i> (Panzer)		5	common	open	
<i>Pseudoophonus rufipes</i> (De Geer)	4	161	common	open	
<i>Pterostichus anthracinus</i> (Illiger)		4		woodlands	moist
<i>Pterostichus caeruleus</i> (L.)	3	102	common	woodlands	
<i>Pterostichus melanarius</i> (Illiger)	52	69	common		
<i>Pterostichus niger</i> (Schaller)	74	16	common	woodlands	moist
<i>Pterostichus oblongopunctatus</i> (F.)	23	6	common	woodlands	moist
<i>Pterostichus strenuus</i> (Panzer)		1	common		
<i>Stomis pumicatus</i> (Panzer)	1				
<i>Syntomus truncatellus</i> (L.)		2	common		dry

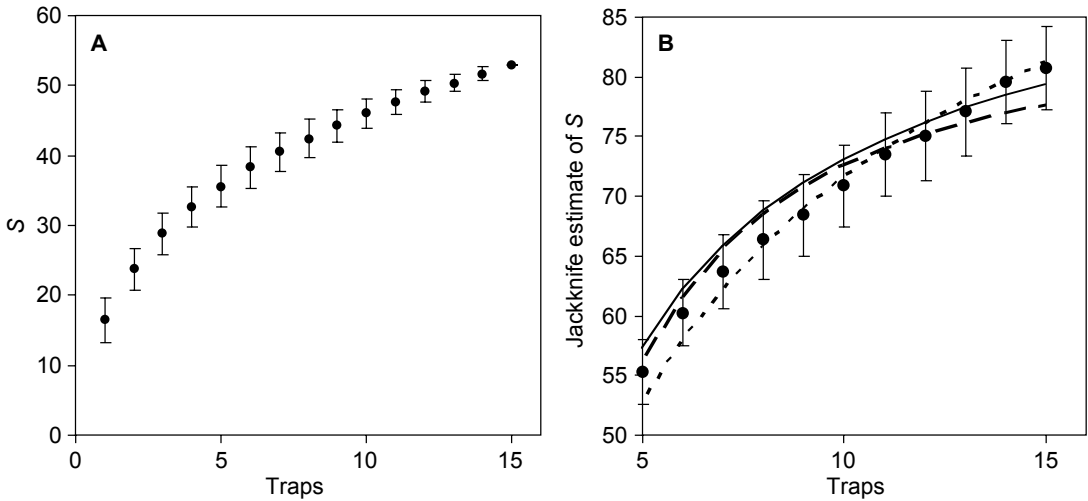
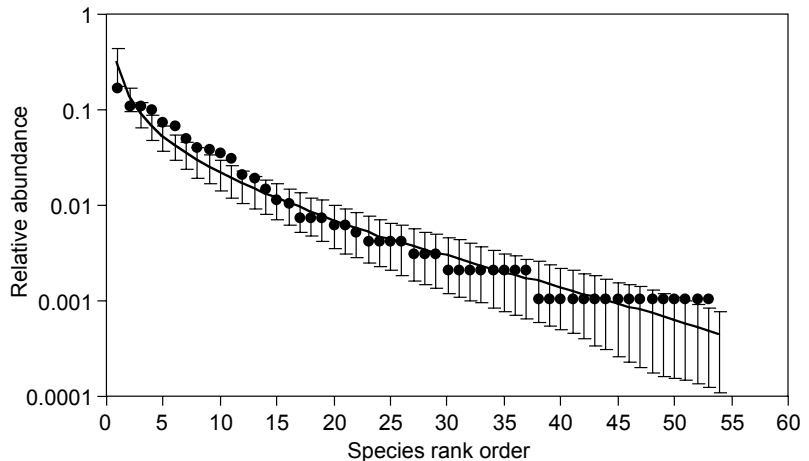


Fig. 1. — **A:** Species accumulation curve of the whole sample. — **B:** The estimate of the species pool size of the second order jackknife estimator did not reach a stable result after successive incorporation of the traps. A fit of this estimate–sample size curve by the asymptotic linear model (Eq. 1) gave a corrected estimate of the species pool size of 92 species (full line). Similar fits by the Monod function (Eq. 2) (pointed line) and by the asymptotic power function model (Eq. 3) (broken line) gave estimates of 111 and 84 species, respectively. Error bars in A and B give one standard deviation obtained after 50 reshufflings of sampling order.

Fig. 2. The species rank order distribution of the total carabid sample is expected to be a sample from the regional species pool. This distribution is best fitted by a Sugihara sequential breakage model with 90 species and a model parameter $k = 0.77$. Error bars give one standard deviation. None of the data points range outside the 95% confidence limits of the model distribution (Tokeshi 1993; data not shown).



model for comparison with the community structures of the four study sites. Using instead species numbers of 111 or 85 shifted the regression line slightly upwards (0.78 ± 0.03) or downwards ($z = 0.75 \pm 0.02$) but did not change the results. All three z values do not significantly deviate from the theoretical expectation of 0.75 ($p(t) > 0.1$). The data points in Fig. 2 were for all three z values inside the 95% confidence limits of the respective model (data only shown for $z = 0.76$).

Species numbers in the poplar plantations were in all cases lower than those in the fields.

We found in both poplar plantations (Wierzbiczany and Ostromecka) 17 species and the same estimation process as above predicted minimum species diversities of 24 ± 3 species for both plantations. In the Wierzbiczany field instead we found 22 species and estimated a total of 31 ± 2 species, while in the Ostromecka field we found 31 species and estimated 41 ± 3 species. In total, we found 29 species in the poplar plantations and 40 species on the fields (Table 1). Of course, the estimates of species numbers might be affected by different sampling efficiencies

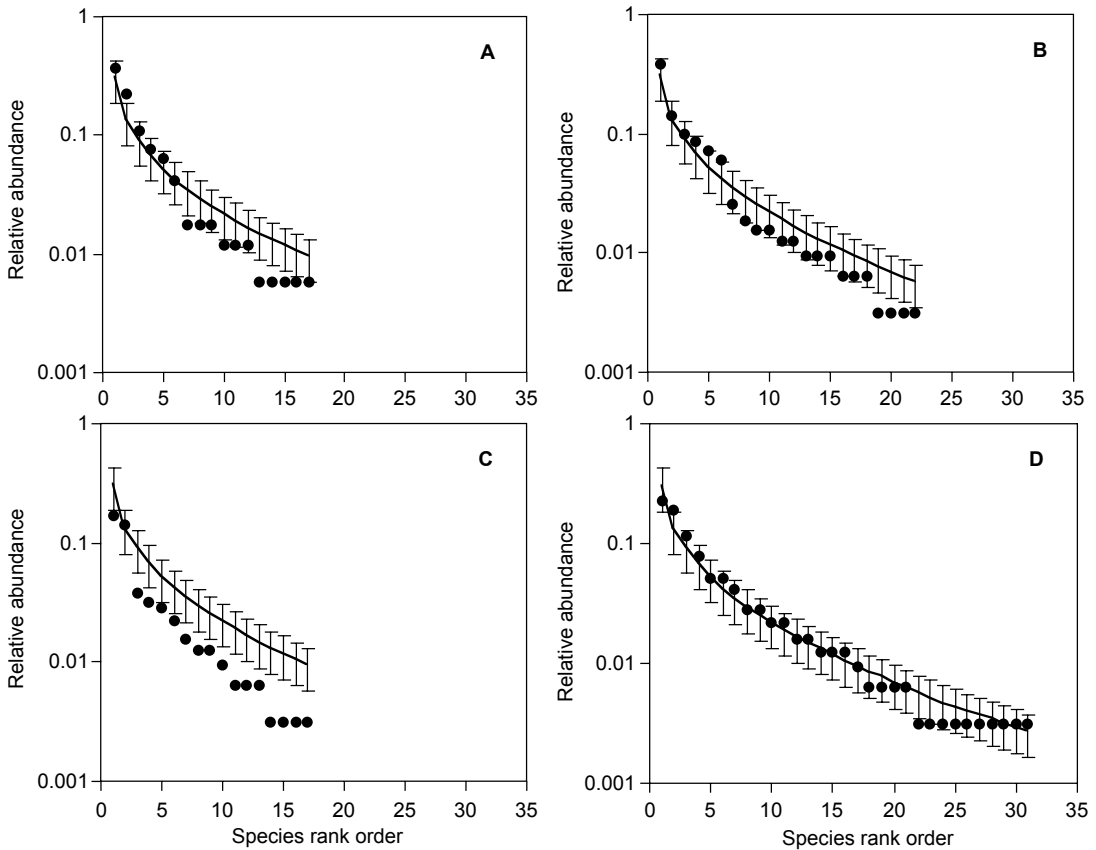


Fig. 3. Species rank order distribution of the carabid fauna of the poplar plantation (A) and the field (B) in Wierzbiczany, and the poplar plantation (C) and the field (D) in Ostromecko. For comparison, the full lines show respective random samples out of a community following a sequential breakage distribution of 90 species. Error bars show 95% confidence limits of the model species relative densities according to the method of Tokeshi (1993).

between fields and plantations due to surface features. To exclude this possibility we also compared the respective species accumulation curves (SACs) at the four sites. According to Lande *et al.* (2000) samples reflect real differences in diversity if the respective SACs do not intersect. When fitted by a logarithmic model ($S = S_0 + z \log n$) the field SACs (Ostromecko: $S = 5.0 + 6.3 \ln n$; Wierzbiczany: $S = 2.1 + 10.5 \ln n$) had at both sites higher intercepts S_0 and slopes z than the plantations (Ostromecko: $S = 0.5 + 5.9 \ln n$; Wierzbiczany: $S = 1.5 + 6.1 \ln n$). From this we conclude that our estimates reflect real differences in species numbers.

A comparison of the species rank order distributions of the four sites with the sequential breakage null model (probability parameter $z = 0.76$) showed that the species rank order distribution

in the poplar plantations was significantly more uneven than expected from a random sample distribution out of a species pool of 90 species. For larger species pool sizes this trend would be even more pronounced. In both cases more than half of the species had relative abundances below the 95% confidence limit of the model distribution (Fig. 3A and C). The field samples instead were closer to the theoretical distribution with the most species rich Ostromecka site not deviating significantly from expectation (only 1 species ranging out of the 95% confidence limit of the model distribution) (Fig. 3B and D). These results point to environmental factors forcing the populations of the plantations away from the null model distribution towards more pronounced dominance rank orders.

Under the assumption that the regional spe-

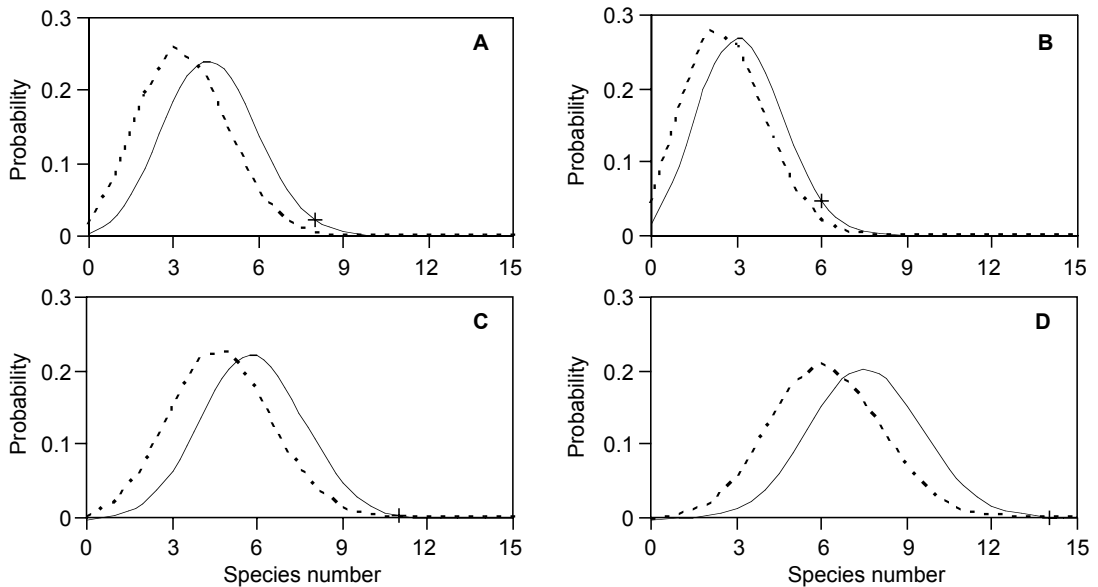


Fig. 4. Probability of finding k species present in both samples of (A) 17 and 22 species (Wierzbiczany: field/plantation); (B) 17 and 17 species (plantation: Wierzbiczany/Ostromecko); (C) 17 and 31 species (Ostromecko: field/plantation); and (D) 22 and 31 species (field: Wierzbiczany/Ostromecko) out of species pools of 90 (continuous lines) and 111 (dashed lines) species. The black squares denote in every case the observed number of species in common. In A, the probability of finding at least 8 species in common is 0.03, in B the probability of finding at least 6 species in common is 0.06, in C the probability of finding at least 11 species in common is 0.005, and in D the probability to find at least 14 species in common is 0.001.

cies pool contains between 90 and 111 species we computed the probability function (Eq. 1) for the number of species common to two habitats k where these habitats have l and m species (the species overlap) (Fig. 3). It appears that the observed species overlap was in all cases more than twice the expected one of the peak probability, and in every case significantly higher than expected by chance (Fig. 4). We found the highest overlap between both fields (Fig. 4D) and the least between the two plantations (Fig. 4B).

The high species overlap between fields and plantations for both study sites (Fig. 4A and C) points to only small faunal differences between field and poplar plantations. The results make the random sample null model improbable.

Species composition

Both the plantations and the adjacent fields were mainly colonized by species that can be classified as common to very common (Table 1). 39 of the 48 identified species (81%) are at least in

semi-moist to moist habitats common to very common. As expected, many of the species (17 out of 48: 35%) are indicators of at least semi-moist habitat conditions. Most abundant were species which prefer shaded habitats like woodlands (*Pterostichus caerulescens*, *P. melanarius*, *P. niger*, and *Platynus assimilis*). *Carabus cancellatus* and *Pseudoophonus rufipes* are typical species of open landscapes and *Nebria brevicollis* is rather ubiquitous. Only two species, *Carabus auratus* and *Atranus collaris*, have to be classified as rare.

On the fields about twice as many individuals were caught as in the poplar plantations (652 : 342). To test whether local carabid abundances in fields and plantations at both study sites were correlated we used rank correlations (Spearman's rank) of species rank order distributions according to the method of Lawton (1984). At both sites abundances of field and plantation species were not correlated: Ostromecko: $r = 0.13$; $p(t) = 0.73$; Wierzbiczany: $r = -0.19$, $p(t) = 0.65$). Field/field and plantation/plantation comparisons instead gave positive correlations although this was for

the plantation/plantation comparison (due to the low number of species in common) non-significant (plantations: $r = 0.48$, $p(t) = 0.32$; fields: $r = 0.58$, $p(t) = 0.03$).

The communities of the four sites were not nested. The nestedness index T was 53.73° . Randomized matrices ($N = 1000$) gave a mean T_{rand} of $41.9 \pm 8.1^\circ$. The probability that the observed temperature was below 20° ($\mu - 2.7\sigma$) was < 0.00003 . The probability of T being $> \mu + 1.44\sigma$ was 0.08.

Standardized co-occurrence indices are Z -transformed and should have a mean of 0 and a standard deviation of 1 (Gotelli 2000). The observed standardized checkerboard index CB that measures the number of species, which never co-occur, had a value of 2.38. There were therefore significantly ($p(\text{CB} > 0) > 0.99$) more perfect species exclusions than expected from 5000 randomized presence-absence matrices. The number of species combinations and the C-score, which is a more liberal measure of species exclusion, did not significantly deviate from expectation of a random assemblage (Checkerboard score = -1.13 , species combination score value = 0).

Species preferring open habitats were more abundant in the fields than woodland species. 17 of 20 species preferring open habitats were found in higher numbers in the fields. But typical woodland species were in more than half of the cases at least as abundant in the fields. Of the 11 species preferring woodlands only 5 were more abundant in the plantations. It is obvious that most abundant species were those that are rather indifferent to humidity conditions (Table 1). Of the 10 species found with more than 30 individuals only two (*Pterostichus niger* and *Platynus assimilis*) prefer moist habitats.

Discussion

Many studies failed to find significant differences in species diversity between agricultural and (semi-)natural habitats at the local scale. Agricultural landscapes seem to act as a filter in accumulating species with overall high abundance and a regional distribution (French & Elliott 1999, French *et al.* 2001). For instance, in a recent and widely cited comprehensive

study on plant, bird, hover fly and bee diversity of agricultural landscapes in the Netherlands, Kleijn *et al.* (2001) found no or only slight diversity differences between monocultures and fields with ecological management agreements to improve landscape heterogeneity. At the local scale extinction of habitat specialists is to a certain extent counterbalanced by higher numbers of ubiquitous species.

For animals in general, and for ground beetles too, comparable studies on poplar plantations are largely missing. However, for plants there is an intensive debate about the role of poplar plantations in contributing to regional biodiversity (Hartley 2002). For instance, Weih *et al.* (2003) found even lower species numbers of plants in young to middle aged poplar plantations and Halpern and Spiess (1995) concluded that poplar plantations of medium to large size have a negative effect on regional plant biodiversity. The present results corroborate this view. Species and individual numbers of the fields were at both study sites higher than in the plantations (Fig. 3). Polish forests, for instance, contain at least 50 species (Huruk 1993, Wojas 1994, 1998, Krzysztofiak 2001). We conclude that poplar plantations neither reach species diversities of at least seminatural forests nor enhance regional species diversity.

The changes in land use from natural to agricultural dominated landscapes during the last centuries had indisputably a major impact on the structure of many animal and plant communities (Andow 1991, Lövei & Sunderland 1996, Gurr *et al.* 2003). The change from highly structured diverse landscape mosaics towards rather monotonous landscapes dominated by mono or at least polycultures has caused the decline of many species with specific habitat requirements (McKinney 1997). Ubiquitous habitat generalists, on the other hand, seem to benefit. This general scheme applies also for carabid beetles for which a series of studies have shown that alteration of land use leads to a continuous decline of habitat specialists while leaving habitat generalists more or less unaffected (Thiele 1977, Turin & Den Boer 1988). In a recent study, Kotze and O'Hara (2003) found that in Belgium, The Netherlands and Denmark 30% to 35% of the specialist carabid species decreased in abundance, while

only 8% to 10% of the extreme generalists did so. The result of such selective local extinction patterns is that species which are able to tolerate (Niemelä 2001) or even to adapt (Niemelä & Spence 1999) to agricultural landscapes reach higher regional distributions and are less prone to becoming regionally extinct.

This leads back to the question whether “renaturalization” and enhancing of local habitat diversity via commercial poplar plantations will enhance regional biodiversity. Our results do not support such a hypothesis. Both the fields and the plantations were nearly exclusively colonized by generalist species. Many of them are characteristic to moist and wet habitats but are apparently indifferent to woodland or open landscape conditions. This result is in line with the findings of Niemelä (2001) and Assmann (1999) who reported specialist species to be nearly exclusively present in old and unfragmented habitats. Specialist species are those which contribute most to regional species diversity. However, the numbers of species reported here for the two plantations and adjacent fields (52 species and an estimated total pool of more than 90 species) do not deviate from numbers found in other rural habitats (Allen 1979, Luff 1987, French & Elliott 1999).

A second aim of the present work was to study whether plantations serve as refuges for ground beetles. Under this hypothesis we expected three patterns. Firstly, there should be a high species overlap between fields and plantations. Secondly, if species regularly migrate between fields and plantations there should also be a correlation in abundance between field and plantation. Lastly, species spatial distribution patterns, represented in presence–absence matrices, should deviate less from random patterns than expected in the presence of structuring forces or even community assembly rules (Gotelli & McCabe 2002). The first prediction is clearly supported by the data. We found for both study sites a much higher species overlap than predicted by chance. However, this high overlap resulted obviously at least in part from the high number of habitat generalists. The second prediction of a correlation between densities is not supported by the data. Species rank order distributions of fields and plantations were clearly uncorrelated.

The four study sites clearly did not form nested subsets of a larger community. In agricultural landscapes nested species occurrence patterns point to ordered species exclusion sequences when reducing habitat size (Doak & Mills 1994). This leads to higher frequencies of habitat specialists and implies that many smaller habitats would be less able to preserve biodiversity than a few larger ones (Armbrecht *et al.* 2001). The lack of nestedness in the present case does neither point to such an interpretation nor to a special preserving value of poplar plantations.

If species regularly migrate between fields and plantations, we expected to find at both study sites higher frequencies of species combinations than expected by chance. The species combination score and the C-score instead did not differ from the null hypothesis of a random pattern. Instead we found a high number of mutual species exclusions as judged by the checkerboard score value of 2.38. The dominance structures differed, with the plantations having the more uneven species rank order distributions (Fig. 3). From this we conclude that both, fields and adjacent plantations, have, despite the high species overlap, different carabid communities.

The above findings do not exclude migrations between fields and plantations and that some of the field species depend on adjacent seminatural habitats as hibernating sites as French *et al.* (2001) suggest. However, we feel that for these processes to be important, community structures of fields and plantations should be more similar than we found. Additionally, species numbers of the plantations should be higher. To test this hypothesis more detailed studies, including capture–recapture experiments, have to be carried out.

There is a potential pitfall in our argumentation due to the number of unrecorded species. This group might contain higher numbers of habitat specialists with restricted regional occurrence. Indeed, for arthropods the positive correlation between regional distribution and local abundance is well documented (Kunin & Gaston 1997). However, as already discussed above for agricultural sites the dominance of generalist species is obvious (Kotze & O’Hara 2003). In the case of the poplar plantations we found at both sites 17 species (only one rare species with restricted habitat requirements, *Atranus collaris*)

and predicted an annual number of 24 species. Even seven additional habitat specialists would not change the overall picture of a species poor community dominated by species with unspecific habitat requirements.

In general, we conclude from the present results that poplar plantations do not contribute to regional ground beetle species diversity. Whether they enhance local carabid diversities in adjacent arable land more than other forms of land use seems at least questionable although we cannot exclude this possibility. Studies on other animal taxa have to show whether both conclusions can be generalized.

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